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RESEARCH ARTICLE

Temporal processing of active and passive head movement

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Abstract The brain can know about an active head movement even in advance of its execution by means of an efference copy signal. In fact, sensory correlates of active movements appear to be suppressed. Passive disturbances of the head, however, can be detected only by sensory feedback. Might the perceived timing of an active head movement be speeded relative to the perception of a passive movement due to the efferent copy (anticipation hypothesis) or delayed because of sensory suppression (suppression hypothesis)? We compared the perceived timing of active and passive head movement using other sensory events as temporal reference points. Participants made unspeeded temporal order and synchronicity judgments comparing the perceived onset of active and passive head movement with the onset of tactile, auditory and visual stimuli. The comparison stimuli had to be delayed by about 45 ms to appear coincident with passive head movement or by about 80 ms to appear aligned with an active head movement. The slow perceptual reaction to vestibular activation is compatible with our earlier study using galvanic stimulation (Barnett-Cowan and Harris 2009). The unexpected additional delay in processing the timing of an active head movement is compatible with the suppression hypothesis and is discussed in relation to suppression of vestibular signals during self-generated head movement.

Keywords Active versus passive · Efferent copy · Multisensory · Sensory suppression · Synchronicity judgments · Temporal order judgments · Time perception · Vestibular

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Introduction

Distinguishing sensory events that originate in the external world from those resulting from our own actions is important for perception and motor control. For example, perceptual stability during head movement is maintained when motor commands are congruent with sensory information from vestibular and other sensory systems. Further, when the head moves it changes the relationship between the observer and the world but what to do about it depends on what it was that caused the change. A deliberate turn of the head to one side requires quite a different response from when the head is displaced by an external agent or an unexpected fall. In the active case, the aim is to change the direction of gaze whereas in the passive condition, gaze should be maintained. Correlated with these needs, the vestibulo-ocular reflex, which serves to stabilize and maintain gaze, is suppressed during an active movement (Roy and Cullen 2002; Cullen et al. 2004). Active and passive head movement are distinguished at the level of the vestibular nuclei where semicircular-canal-related activity is substantially less during active head movement than during the equivalent passive movement (Boyle et al. 1996; McCrea et al. 1999; Roy and Cullen 2001; Cullen et al. 2011). Here we assess whether this distinction might

appear as a difference in the time it takes to become aware of active and passive head movement.

A possible mechanism for differentiating active and passive movements is by the use of a "corollary discharge" (Sperry 1950) or an "efference copy" (von Holst and Mittelstaedt 1950) of the motor command that can be used by sensory areas to suppress the sensory consequences of motor action. Such a signal can affect the way in which sensory information is processed allowing the observer to be prepared for the sensory consequences of their actions. Under lab conditions this can produce transient distortions in the perception of space (Duhamel et al. 1992, Ross et al. 1997; see Ross et al. 2001 for a review) and time (Williams et al. 1998; Haggard and Whitford 2004; Morrone et al. 2005; Winter et al. 2008) around the time of a movement. An internal model of the sensory consequence of moving the head, derived from an efference copy, appears to be responsible for suppression of the responses of vestibular nucleus neurons known to be involved in postural control and spatial orientation (Roy and Cullen 2004; Cullen et al. 2011).

If an internally derived signal precedes head movement and is accessible to the mechanism(s) used in determining the time of onset of an active head movement, then such a head movement may be more speedily perceived than a passive head movement where timing information has to be derived from sensory feedback. For example, it has been shown that estimates of movement onset precede recorded movement onset by about 80 ms (Libet 1985; Haggard et al. 1999; Obhi et al. 2009), suggesting that awareness of action might be linked to pre-motor processing which in turn may explain anticipatory awareness of action (Blakemore et al. 2002). Anticipation of active head movement onset may thus reduce the delay in processing vestibular information and also increase timing judgment precision. We refer to this as the *anticipation hypothesis*. Alternatively, if perceived timing depended on sensory feedback (Aschersleben and Prinz 1995; Aschersleben et al. 2001, 2004), the perceived onset time might be delayed as a consequence of the suppression of vestibular nucleus activity. We will refer to this as the *suppression hypothesis*. We assessed these competing hypotheses by comparing the perceived onset of active and passive head movements with the perceived timing of touch, light and sound reference stimuli.

Materials and methods

Participants

Fifteen participants (9 males) aged 24–45 years including one author (MB-C) participated in this study and gave informed written consent according to the guidelines of the York University Research Ethics Board in compliance with the 1964 Declaration of Helsinki. Participants reported no auditory, visual, vestibular or other neurological disorders. Participants received no feedback regarding their performance in any of the experiments. All participants were rewarded with chocolate for their participation.

Head movement recording and analysis

Head movement was monitored using a velocity transducer (Watson Industries Inc. Rate Sensor, ARS-C251-1ARP, Eau Claire, WI, USA) mounted on a headband (Fig. 1) and oriented so that it was activated by yaw movement of the head. Signals from the rate sensor were fed to a Cambridge Electronic Design 1401 computer system (CED1401; Cambridge, England) controlled by a PC, which was also used to control presentation of all stimuli and to record responses. The onset of head movement was defined in post hoc analysis as having occurred when the head moved at a velocity greater than 2 standard deviations from the average head velocity recorded in the first 100 ms of each trial while the head was stable. Trials in which the head moved during the first 100 ms of the trial were eliminated. In order to equate active and passive head movements, active head movement trials in which peak acceleration exceeded the maximum peak acceleration for passive head movement and passive head movement trials in which peak acceleration was less than minimum peak acceleration for active head movement were eliminated (16 and 10% total data loss of active and passive head movement trials respectively).

Head movement generation

Passive head movement (HM_P) was executed by the experimenter who placed his hands on the sides of the participant's head and quickly rotated the head rightward by about 10° and back to a straight ahead position (Fig. 1a). The experimenter kept their hands on the participant's head throughout each block of trials and applied constant pressure using a firm grasp of the head. Participants were instructed to relax and not to resist the movement. Active head movement (HM_A) was self-generated by participants (Fig. 1b) in response to an LED in the case of HM_A-sound and HM_A-touch trials or a sound for HM_A-light trials. Participants were instructed to rotate their heads in a way similar to the movement generated passively by the experimenter in practice trials.

Touch, light and sound generation

Touch stimuli consisted of 50 ms bursts of 200 Hz vibration using a tactile vibrator held between the index finger

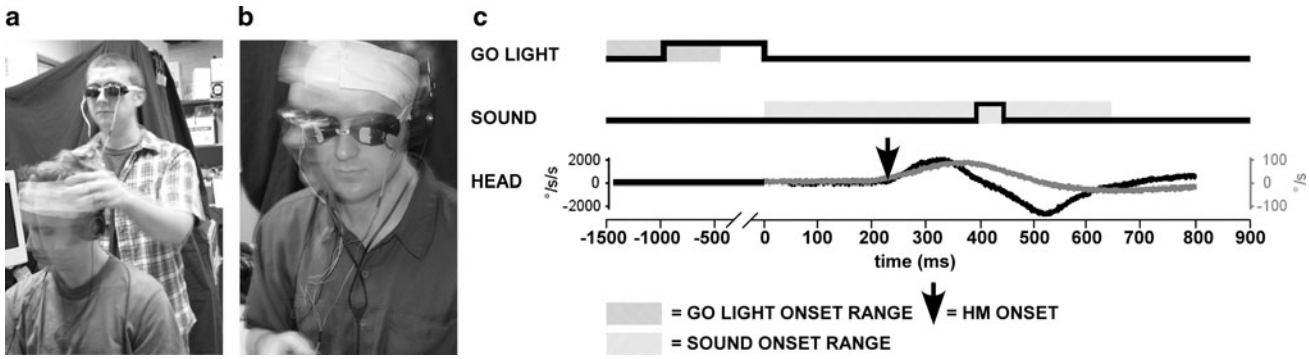

Fig. 1 Experimental procedure. **a** Time-lapse photograph of passive head movement paired with a sound stimulus delivered through headphones. Here the experimenter rotates the participant's head in response to go light offset presented via goggles. **b** Active head movement paired with sound. Here the participant rotated their own head in response to go light offset. **c** Trial design schematic. The trial begins with the offset of a go light signal. The onset of a 50 ms sound occurred anywhere from 0 to 650 ms thereafter. The two traces show the acceleration (*black line*, *left-hand scale*) and velocity (*gray line*, *right-hand scale*) of a typical head movement. The point of onset of head movement (indicated by the arrow) was defined in post hoc analysis (see "Materials and methods")

and thumb of the right hand. For light stimuli, participants sat under a hemispherical ganzfeld dome and received a diffuse flash from an externally mounted strobe light lasting approximately 40 microseconds. Sound stimuli consisted of 50 ms bursts of 2,000 Hz, 73 db tones using headphones. Further details can be found in Barnett-Cowan and Harris (2009). Participants wore ear plugs during all tasks, even during sound trials, in order to mask noise generated by the strobe and vibrator while still being able to hear the sound stimulus. The comparison stimulus property parameters were selected to be well above threshold so that time to detect each stimulus would be minimal.

Procedure

Figure 1c schematically shows how stimuli were presented in each trial. Head movement was made following the offset of a "go" light which event also triggered a comparison light, sound or touch stimulus. Because of the reaction time before the head movement commenced, comparison stimuli could be presented before or after the head movement (c.f., Winter et al. 2008). Passive head movement was executed manually by the experimenter also in response to the offset of a "go" light (see Fig. 1). A touch, light or sound stimulus was presented between 0 and 650 ms after the "go" light offset. No significant difference ($t_{89} = 1.37$, $P = 0.174$) was found between the reaction times to make an active or passive head movement after go light offset (177 ms, s.d. 37 ms; 185 ms, s.d. 55 ms, respectively) so that the comparison stimuli were presented over a comparable range of times relative to the onset of passive and active head movement.

Two types of judgments were made, each in separate blocks: temporal order judgments and synchronicity judgments. For temporal order judgments (TOJ), participants were asked "which stimulus appeared first?" Participants responded by lifting their left foot to indicate "touch, light or sound first" or their right foot to indicate "head movement first." For synchronicity judgment (SJ) trials, participants were asked "were the stimuli synchronous or not?" Participants responded by lifting their right foot to indicate "synchronous" or their left foot to indicate "not synchronous." Participants were instructed to attend equally to head movement and the other stimulus being presented. Both TOJs and SJs were used to identify the amount of asynchrony required for stimulus pairs to appear simultaneous as these tasks often yield different estimates of precision (Mitrani et al. 1986; Vatakis et al. 2008; Barnett-Cowan and Harris 2009).

Twelve conditions were run in a block design with 120 trials in each block. The conditions were passive or active head movements compared to touch, light or sound. Each condition was run twice, once to obtain TOJs and once for SJs. Participants kept their eyes closed during touch and sound blocks and open during light blocks. Data collection took approximately 10 min for each block. Participants were allowed to take as long as they needed to make their judgments. The order of conditions was randomized across participants and testing occurred over the course of several non-consecutive days.

Data analysis

For both TOJs and SJs, the percentage of trials on which a particular response was chosen was plotted as a function of SOA with negative SOAs indicating that the head moved prior to the other stimulus. A two-parameter, cumulative Gaussian (Eq. 1) was fitted to the TOJ data and a three-parameter Gaussian (Eq. 2) was fitted to the SJ data.

$$y = \frac{100}{1 + e^{-\frac{(x-x_0)}{b}}}\% \quad (1)$$

$$y = a \cdot e^{(-0.5(\frac{x-x_0}{b})^2)} \quad (2)$$

The inflection points of the cumulative Gaussians (x_0 for TOJs, Eq. 1) or the peaks of the Gaussians (x_0 for SJs, Eq. 2) were taken as the point of subjective simultaneity (PSS). The standard deviation (b) was taken as the JND. "*a*" is a scaling factor. These values were submitted to repeated measures ANOVA. The Greenhouse–Geisser correction was used for any violations of the assumption of sphericity.

Results

Passive head movement

On average, passive head movement displacement was 11° (SD: 4.1), with a peak velocity of 95°/s (SD: 28.8), peak acceleration of 1,166°/s/s (SD: 363) and peak jerk of 19,260°/s/s/s (SD: 6,461; see Fig. 2). Latencies relative to head movement onset for peak velocity, acceleration and jerk were 113.2 ms (SD: 22.4), 79.3 ms (SD: 17.6) and 58.4 ms (SD: 16.1), respectively.

The TOJs and SJs made for passive head movement are shown in Fig. 3. The average PSSs derived from TOJs and SJs for passive head movement are shown in Fig. 3b. A 2 (task: TOJ PSS and SJ PSS) × 3 (modality: touch, light, sound) repeated measures ANOVA revealed no significant effects of task ($F_{(1,14)} = 1.8$, $P = 0.202$) or modality ($F_{(2,28)} = 1.2$, $P = 0.312$) and the task-by-modality interaction did not reach significance ($F_{(1.437,20.115)} = 3.0$, $P = 0.089$). All TOJ and SJ PSSs were significantly different (one sample t-tests, all $P < 0.01$) from true simultaneity requiring sensory stimuli to be presented 44.8 ms (6.3 s.e.) on average after the head movement to be regarded as simultaneous, with the exception of TOJs for passive head movement paired with touch ($P > 0.05$) which were perceived as simultaneous when presented with 0 delay.

The mean JNDs derived from TOJs and SJs for passive head movement are compared in Fig. 3c. A 2 (task: TOJ PSS and SJ PSS) × 3 (modality: touch, light, sound) repeated measures ANOVA revealed a significant main effect for task ($F_{(1,14)} = 8.3$, $P = 0.012$) but not for modality ($F_{(2,28)} = 0.8$, $P = 0.459$) and the task-by-modality interaction did not reach significance ($F_{(2,28)} = 3.0$, $P = 0.084$). These results indicate that, in general, participants were less precise when making synchronicity judgments than when making temporal order judgments.

Active head movement

On average, active head movement displacement was 26.5° (SD: 9), with a peak velocity of 159°/s (SD: 44), peak acceleration of 1,678°/s/s (SD: 470) and peak jerk of 27,331°/s/s/s (SD: 8,217; see Fig. 2). Latencies relative to head movement onset for peak velocity, acceleration and jerk were 143.2 ms (SD: 26.9), 80.3 ms (SD: 16) and 53.9 ms (SD: 11.2), respectively.

The results of TOJs and SJs made for active head movement are shown in Fig. 4. The average PSSs derived from TOJs and SJs for active head movement are shown in Fig. 4b. All TOJ and SJ PSSs were significantly different from true simultaneity such that stimuli needed to be presented 79.3 ms (6.5 s.e.) on average before the head movement (one sample t-tests, all $P < 0.01$). A 2 (task: TOJ PSS and SJ PSS) × 3 (modality: touch, light, sound) repeated measures ANOVA revealed no significant effects of task ($F_{(1,12)} = 0.4$, $P = 0.529$), modality ($F_{(2,24)} = 0.1$, $P = 0.876$) and the task-by-modality interaction did not reach significance ($F_{(2,24)} = 3.1$, $P = 0.062$). These results indicate that, in general, active head movement must be executed before a touch, light or a sound by approximately 80 ms in order for the sensory stimulus to be perceived as simultaneous with the head movement.

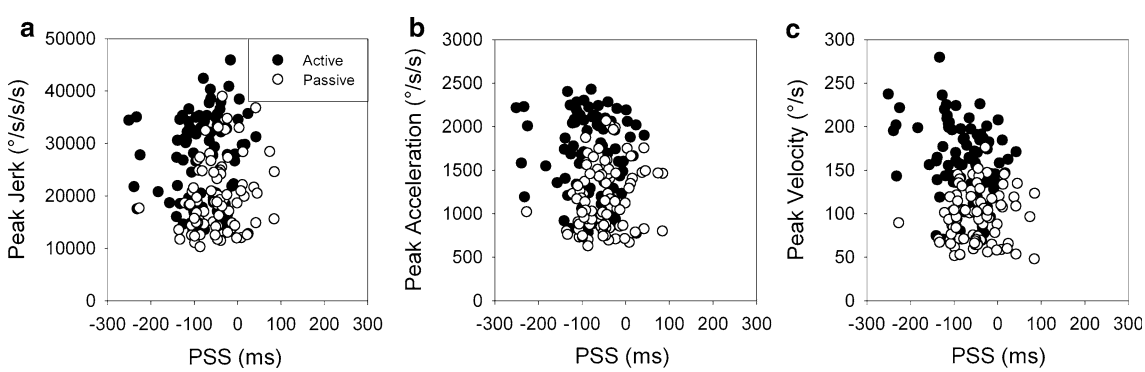

Fig. 2 Passive versus active head movement properties. Peak jerk (**a**), acceleration (**b**) and velocity (**c**) plotted as a function of PSS

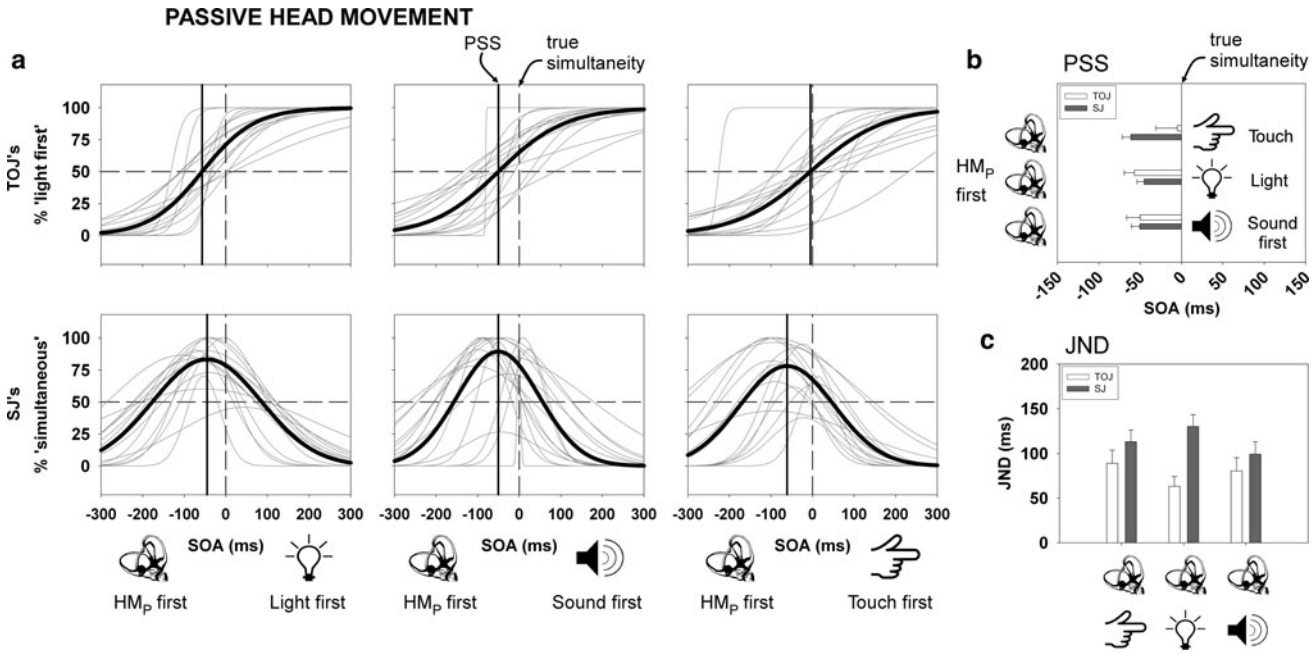

Fig. 3 Perceived timing of passive head movement (HM_P). **a** Average TOJ cumulative Gaussian (*top row*) and SJ Gaussian (*bottom row*) curves for judgments of the relative timing of passive head movements and other reference stimuli. The three pairs of graphs are arranged according to stimulus pair (HM_P-light, HM_P-sound and HM_P-touch) where positive and negative SOA values mean whether the head movement (−ve) or reference stimulus (+ve) was presented first, as shown by the inserted cartoons. The individual participants' curves (*gray lines*) are best fits through the means of the percentage of times one was perceived to be first, *plotted* as a function of SOA. The *thick black curves* are reconstructed from the average PSS's and JND's of the participants. The *solid vertical lines* represent the average PSS. The *dashed vertical lines* represent the point of true simultaneity (SOA = 0 ms). **b** PSS data plotted as a function of SOA. **c** JND data plotted as a function of SOA. *Error bars* are ±1 s.e.m

The mean JNDs derived from TOJs and SJs for active head movement are compared in Fig. 4c. A 2 (task: TOJ PSS and SJ PSS) × 3 (modality: touch, light, sound) repeated measures ANOVA revealed a significant main effect for task ($F_{(1,12)} = 13.4$, $P = 0.003$) but not for modality ($F_{(2,24)} = 0.8$, $P = 0.460$) or for a task-by-modality interaction ($F_{(2,24)} = 0.1$, $P = 0.864$). These results, like those found for passive head movement, indicate that participants were less precise when making synchronicity judgments than when making temporal order judgments.

Active versus passive head movement

While the range of head movement displacement for active (8 : 44°) and passive (4 : 24°) head movement were quite different, ranges for velocity (70 : 279°/s; 47 : 176°/s), acceleration (783 : 2422°/s/s; 623 : 2061°/s/s) and jerk (13066 : 45787°/s/s/s; 10189 : 38852°/s/s/s)—which are more relevant for information pertaining to head movement onset—were reasonably well equated (see Fig. 2). Significant mean differences were found, however, when comparing active and passive head movement using paired t-tests for peak velocity ($t_{(84)} = 11.2$, $P < 0.001$), acceleration ($t_{(84)} = 8.4$, $P < 0.001$) and jerk ($t_{(84)} = 7.8$, $P < 0.001$).

The 2 (head movement: passive and active) × 2 (task: TOJ PSS and SJ PSS) × 3 (modality: touch, light, sound) repeated measures ANOVA used to determine differences in PSS between types of head movement revealed a significant main effect of head movement type ($F_{(1,12)} = 16.3$, $P = 0.002$) and a significant head-movement-by-task-by-modality interaction ($F_{(2,24)} = 5.9$, $P = 0.008$) which was driven by the TOJ estimates for passive head movement paired with touch that were near actual simultaneity (see above). No other effects were significant.

These results indicate that, in general, the delay associated with passive head movement was significantly shorter than the delay associated with active head movement. In other words, active head movement needed to occur a further 35 ms before a touch, light or a sound, in addition to the 45 ms required for passive head movement, in order for the stimulus pair to be perceived as simultaneous (Fig. 5a).

The peak velocity of our active head movements was significantly negatively correlated with PSS (slope: −0.18, $r = -0.236$, $P = 0.028$; Fig. 5b) as was peak displacement (slope: −0.04, $r = -0.280$, $P = 0.009$). Critically, no significant correlation was found for peak velocity with passive head movements and no correlations were found between peak jerk, acceleration and PSS for either active or

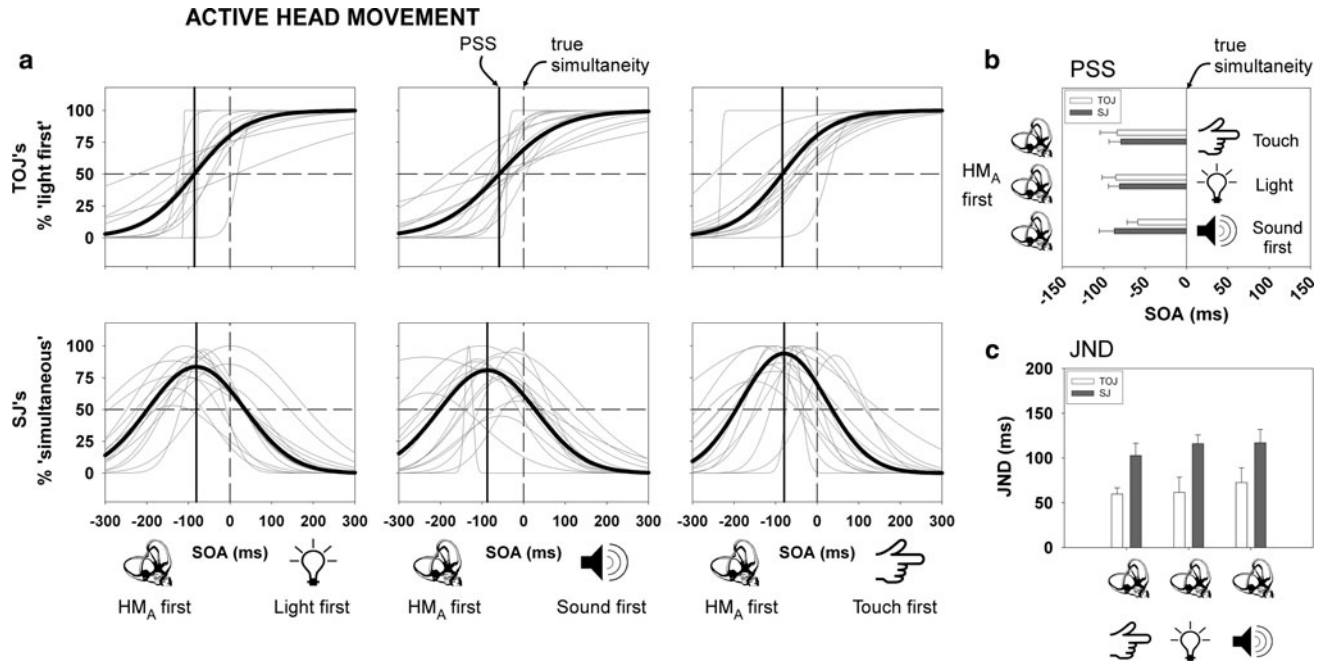

Fig. 4 Perceived timing of active head movement (HM_A). Conventions as in Fig. 3

passive head movements. This indicates that the PSS difference between active and passive head movement cannot be attributed to differences in movement profiles between these two classes of head movement.

The 2 (head movement: passive and active) × 2 (task: TOJ PSS and SJ PSS) × 3 (modality: touch, light, sound) repeated measures ANOVA used to determine differences in JND between types of head movement revealed a significant main effect of task ($F_{(1,12)} = 16.0$, $P = 0.002$) indicating that participants were less precise when making synchronicity judgments than when making temporal order judgments (Fig. 5c). No other effects were significant.

Discussion

The results of this study suggest that the efference copy associated with an active head movement does not give the perceived timing of an active head movement a significant advantage over the perceived timing of a passive head movement when compared to other sensory stimuli. That is, the anticipation hypothesis is not supported. Rather, consistent with the suppression hypothesis, information concerning active head movement appears to be available to perception even later than information concerning passive head movement, requiring an additional 35 ms to reach awareness (see Fig. 4a).

What is it that takes this extra 35 ms? Previous research in our lab (Winter et al. 2008) found that active touch is perceived as simultaneous with passive touch when an active touch leads a passive touch by 29 ms. Similar results were found by Lau et al. (2004) and Obhi et al. (2009) when comparing the relative perceived timing of self-generated movement with a clock used as an external visual reference. We suggest that this 35 ms delay arises from a sensory suppression which occurs during active movement (Williams et al. 1998). Our hypothesis is that the suppressed signal (in this case, vestibular) takes longer to reach threshold than a stimulus that is not suppressed.

An alternative explanation to account for the difference in PSS between active and passive head movement is that participants did not judge synchronicity relative to head movement onset defined as a change in velocity but rather relative to a different cue for example, peak acceleration. Indeed, since the time an active head movement took to reach peak acceleration was about 80 ms, this meant that peak head acceleration did occur at about the same time as comparison stimuli judged to be simultaneous with active head movement. However, the time it took passive head movements to reach peak acceleration was also around 80 ms while the PSS was around 45 ms: some 35 ms earlier. Thus, it remains curious that when efference copy is available in advance of an actual head movement, it does not make knowledge of the timing of the head movement any more accurate (it actually got worse by 35 ms) or precise (there was no difference between the active and passive JNDs).

External touch applied to the finger has been shown to slow modulate the perceived timing of finger movement (Obhi 2007; Obhi et al. 2009). We were thus concerned

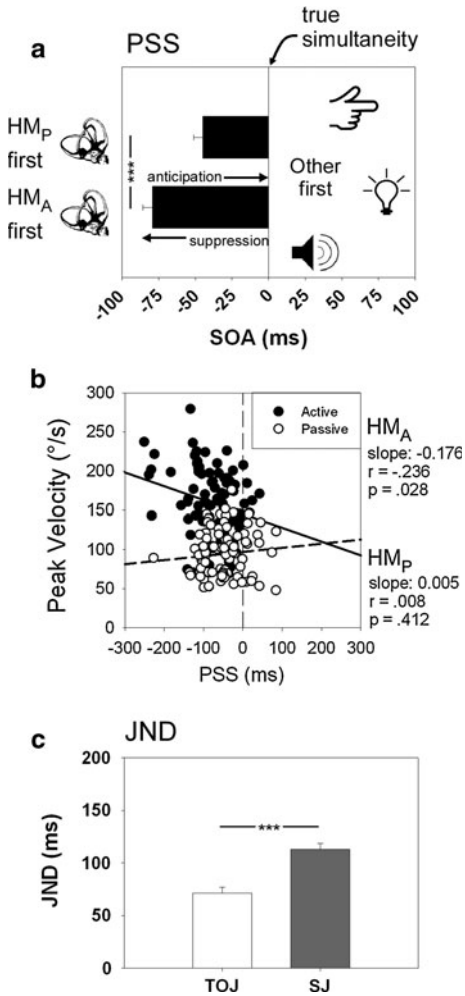

Fig. 5 **a** Overall average PSS data from Figs. 3b and 4b showing that for HM_P the head must move by 45 ms before other stimuli in order to be perceived as simultaneous. Consistent with the "suppression" hypothesis and inconsistent with the "anticipation" hypothesis, an additional 35 ms was required for HM_A. **b** Linear regression fits to peak velocity as a function of PSS from Fig. 2c. **c** Average JND data from Figs. 3c and 4c. *Error bars* are ±1 s.e.m. ***$P < 0.001$

that the presence of force applied to the skin of the head when the head was moved passively may have provided additional information about the onset of the passive movements. Indeed, the TOJ PSS for passive head movement paired with a touch was essentially at the point of actual simultaneity suggesting that participants could have compared touch applied to the head with touch applied to the finger. However, the SJ PSS for passive head movement paired with a touch was delayed along with other stimulus pairings arguing against this. Further, if participants used such additional information about head movement onset, we would have expected a decrease in JND for passive compared to active head movement. This was not the case (compare Figs. 3c, 4c). Finally, while touch has been shown to modulate the perceiving timing of finger movements, the effect could not explain our differences as arising from touch cues being present only during our passive movements. When touch was provided to the finger for passive and not active movement (comparable to pressure being applied to the head only for passive movements in the present study), no difference was found in timing estimates (Obhi 2007). When touch was provided for both active and passive movement, active finger movement was perceived as occurring earlier than passive finger movement by about 20 ms (Obhi et al. 2009) suggesting that touch may have speeded the perception of active movement but not affected passive movement. Taken together, these results suggest that the difference in the perceived timing of active and passive head movement is not likely attributable to differential application of touch to the head but rather to differential processing of vestibular information evoked by active compared to passive head movement.

Our overall conclusion is that perceptual knowledge of active head movements is suppressed in line with suppression of vestibular nucleus activity (Boyle et al. 1996; McCrea et al. 1999; Roy and Cullen 2001; Cullen et al. 2011) and vestibularly evoked eye movements (Roy and Cullen 2002; Cullen et al. 2004). This conclusion is also in agreement with previous studies which have shown that the sensation of touch is suppressed during an active movement (Williams et al., 1998; Haggard and Whitford 2004). Discrepancies between the present study and that of Obhi et al. (2009), who found evidence that both efferent and reafferent signals affected conscious awareness of finger movements, may be explained by the fact that vestibular suppression is not complete (see also Haggard and Whitford 2004). Indeed, the gain [(spikes/sec)/(deg/sec)] reported by Roy and Cullen (2004) for suppression of vestibular afferent signals (0.86) based on head movement velocity is very similar to the significant modulation of the PSS with peak head movement velocity that we report here (1−slope = 0.82; see Fig. 5b).

What might be the function of such sensory suppression? The brain must distinguish between sensory events that are externally induced and those that are self-generated in order to maintain perceptual stability and produce coordinated behavior. Suppression of sensory signals arising from self-generated movement has been shown to be necessary to maintain perceptual stability (Watson and Krekelberg 2009). This is apparent during a self-generated saccadic eye movement (Matin 1974; Burr et al. 1999) which could potentially otherwise be interpreted as a swing of the entire world at high velocity. Similarly, vestibular activity during an active head movement need not (and should not) evoke corrective eye movements such as the vestibulo-ocular reflex. An intact vestibulo-ocular reflex is essential for stabilizing gaze while our head bops up and

down during walking, but can be counterproductive during a voluntarily head movement made to redirect gaze. Vestibular reflexes (McCrea et al. 1999) and their underlying signals (Roy and Cullen 2001, 2002, 2004) are suppressed during active movement of the head. The increased delay for perceiving a head movement may thus be an additional consequence of this suppression.

That passive and active head movements both had to occur prior to touch, light and sound stimuli in order to be perceived as simultaneous, confirms our previous observation (Barnett-Cowan & Harris 2009) in which galvanic vestibular stimulation needed to occur substantially before other stimuli to be perceived as simultaneous with them. A recent study by Sanders et al. (2011) also found that passively evoked vestibular stimulation had to occur substantially before a reference sound stimulus. When expressed as relative to detection threshold (Heerspink et al. 2005), Sander's et al.'s data suggest that vestibular stimulation has to occur prior to sound by ~120 ms. In summary, therefore, artificial stimulation of the vestibular system yields delays of 160 ms relative to a reference stimulus (Barnett-Cowan and Harris 2009), low-amplitude passive vestibular stimulation yields delays of 120 ms (Sanders et al. 2011) and natural head movement reported here yields delays of 45–80 ms (present study). The increased speed of response during natural head movements may be due to head movement intensity differences between those used by Sanders et al. and the present study and/or the addition of proprioceptive inputs from the neck muscles and joints which were used here (Biguer et al. 1988; Roll et al. 1991; Taylor and McCloskey 1991; Fitzpatrick and Day 2004).

Although efference copy information does not facilitate the perceived timing of head movement, performance in spatial updating has been shown to be better following self-generated movement than after passive rotation (Blouin et al. 1998; Jurgens et al. 1999). The unexpected additional delay in the perceived timing of self-generated movement we report here, despite available efferent information occurring in the cortex considerably before perceptual reports, thus represents an important caveat when interpreting brain activity thought to underlie movement and timing perception. Our suggestion is that efference copy is available for spatial perception and to suppress self-generated sensory information, but it is inaccessible to the mechanism(s) underlying the perception of head movements.

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