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Modification of magnitude estimations in thermotactile perception during self-generated and externally generated movements

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Abstract. Fourteen participants felt a 'cold' stimulus move across a fingertip. When movement was self-controlled, the stimulus was reported as feeling less 'cold' than when movement was externally generated.

1 Introduction

Nelson (1996) suggests that signals from self-generated actions appear to "suppress sensory responsiveness and, thus, probably perception" (page 807). Similarly, Blakemore et al (2000) imply that the sensory effects of a movement can be attenuated by the prediction of future movements. If this is the case, will the perception of temperature be affected by self-generated and externally generated movement?

A physiological account of 'cold' perception would include reference to the activity of thinly myelinated Aδ fibres and a raised intracellular level of calcium (Ca^{2+}) when a cold ($\sim 15\,^{\circ}$C) stimulus is applied (Bessou and Perl 1969; Lamotte and Thalhammer 1982; Saumet et al 1985; McKemy et al 2002; Okazawa et al 2002). In an ambient indoor climate (eg 20 – 22 °C), a healthy human's skin temperature is maintained at 30 – 36 °C (Jones and Berris 2002; Kenshalo and Scott 1966). However, for temperatures lower than 20 °C, a continuous cool sensation is perceived (Jones and Berris 2002).

Although neurophysiological research reveals much about thermal perception, aspects other than physiology have been implicated as well. One variable that may lead to differential perception, despite identical receptor states, is self-generated versus externally generated movement. According to some theorists, perceptual awareness may be modulated by cues from self-generated actions (Blakemore et al 1998b; Bolanowski et al 2001). It has been postulated that the ability to distinguish self-generated from externally generated percepts is the result of an internal 'forward model' (Sperry 1950; Decety 1996). Forward models are presumed to capture the causal relationship between actions, as signalled by a 'corollary discharge' mechanism, and the predicted sensory outcome (Blakemore et al 1998b).

One of the earlier authors to acknowledge the importance of the concept of corollary discharge was Von Holst (1954) who suggested that it was a copy of the motor command from central motor networks. Corollary discharge theory was originally established as an explanation of the ability to distinguish self-generated actions from external percepts in the visual system (eg Sperry 1950; Von Holst 1954). In relation to vision, the optical images associated with self-generated eye movements are perceived as being stationary (Kudo et al 2004). This is explained in terms of the self-generated action producing a copy of the movement command (corollary discharge) which is subtracted from the retinal motion signal (Haarmeier et al 1997; Ford et al 2001). The comparison of the corollary discharge signal with actual motor feedback cancels self-induced sensory changes (Ford et al 2001) and thus "[animals] do not mistake the shift of the image projected onto the retina for motion of the world around [them]" (Haarmeier et al 1997, page 849).

A mechanism for distinguishing self-generated from externally generated percepts has emerged as an important theoretical concept in tactile research. Muscular afferent signals are contrasted with the expected sensory consequences of motor output and utilised by "sensory systems to adjust for resultant changes to peripheral receptors and by motor planning systems to prepare subsequent movements" (Sommer and Wurtz 2002, page 1480). Accordingly, there may be two roles of corollary discharge: helping us discriminate and respond to signals from the mix of self-generated actions and the environment (Carlsson et al 2000; Poulet and Hedwig 2002), and supplying a pre-estimation of, and making fine adjustments to, ongoing motor commands (Ito 1970; Gellman et al 1985; Carlsson et al 2000).

The purpose of this experiment was to investigate the effects of self-induced versus other-induced movements on the interpretation of 'cold' stimuli. Consistent with previous research on the consequences of stimulus predictability (eg Blakemore et al 1998a), it was hypothesised that there would be a reduction in the magnitude estimation (ME) of a 'cold' temperature when movement was self-generated.

2 Method

2.1 *Participants*

A convenience sample consisting of seven women and seven men participated in the experiment. No participant had a current or past neurological impairment, nor were they familiar with the experimental tasks or the hypothesis being tested. Participants were aged between 19 and 48 years (mean = 25 years, SD = 8.63).

2.2 *Materials*

The thermal stimulus device (TSD) consisted of a solid-state $30 \times 30 \times 4.7$ mm^3 CP1.4-71-10L series thermoelectric cooler (TEC) attached to a $125 \times 80 \times 0.5$ mm^3 piece of aluminium. The aluminium served as a heat sink and was fastened to a piece of dowel (length 30 cm), which could be moved horizontally (see figure 1). The TEC (shown in hidden detail in figure 1) contains numerous p – n pairs (couples) electrically connected in series and compressed between two non-metallised ceramic plates. The CP1.4-71-10L series functions within the limits of 3.90 A, 18.70 W, and 8.60 V. The TEC was connected to a Powertech™ MP 3081 DC power supply. Upon application of DC current to the TEC, heat is transferred across the TEC creating opposing cold and hot sides.

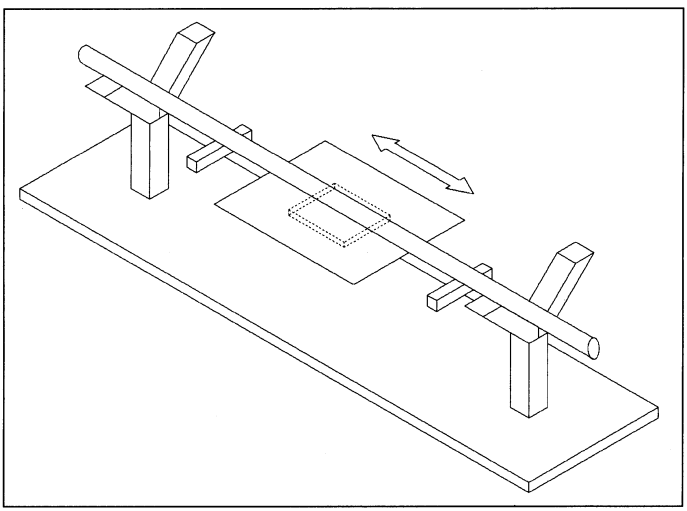

Figure 1. Thermal stimulus device (TSD).

The back and forth movements of the TSD were limited to 2.5 cm in length. The dowel could be moved by either the participant using the index finger and thumb of the left hand or, from the other end, by the experimenter. Pushing or pulling the dowel allowed the TEC to be passed over the participant's right index finger during the experiment.

2.3 *Procedure*

A procedure similar to one previously reported by Blakemore et al (1998c) was used. In each condition, participants were seated with their right hands placed on a table, palm up, keeping their index fingers outstretched and the other digits flexed. The TEC was placed centrally in front of the participant. For each stimulus presentation, blindfolded participants were instructed to place the pad of their right index fingers onto the TEC. Participants were given clear instructions about the nature of each condition, told which task to perform, and advised that stimuli would always be 'cold'.

In condition 1 (self-produced movement), the participant was instructed to use her/his left index finger and thumb to perform regular (on average every 2 s) horizontal movements of the TSD rod, so that the TEC moved across the stationary right index finger. Participants were given practice trials beforehand, without cold, to ensure that they could reliably reproduce the movements made by the experimenter. In condition 2 (externally generated 'cold' stimulation), the participant kept both hands stationary while the experimenter moved the 'cold' stimulus across the participant's right index finger.

The two conditions were administered within-subjects with three replications of each condition per participant, creating a total of six trials. In all conditions, an ME was recorded immediately after exposure to the stimulus. Participants were instructed to make a mark on a solid black line (10 cm in length) that best represented the perceived coldness on each trial. A fresh form was used for each trial. This first mark may have been used as a reference point for subsequent judgments. However, for all trials, participants were free to put a mark at any point along the scale. If no 'coldness' (ie room temperature) was perceived on a given trial, the participant was instructed to mark 'zero' (ie the left-most position on the line). Inclusion of this response option was necessary to ensure that coldness was actually detected. The right-most position of the line was to represent a 'very cold' temperature.

Thermal stimuli lasted 10 s and the interstimulus-onset interval (ISI) was 90 s. During the ISI the DC power supply was preset to 1 A, 3 V and switched on 5 s prior to trial commencement. The 'coldness' was therefore equal across trials.

2.4 *Design*

The experiment was a 2×3 within-subjects design with two factors (externally generated versus self-generated movement) and three trials in each condition. Stimulus sequences were randomised and counterbalanced within and between participants. The measured (dependent) variable was perceived 'coldness'.

3 Results

Table 1 presents descriptive data (means and standard deviations) for the MEs of 'cold' temperatures. As the underlying assumption of sphericity (Mauchly's) was met, parametric statistics were used in the analysis of participant's response data. Sphericity is an assumption of repeated-measures designs that can be viewed as an extension of the homogeneity-of-variance assumption essential in independent-measures ANOVAs. For sphericity to be met, the observed sample variances of the difference needed to be relatively equal.

The data in table 1 indicate that self-generated movement attenuated subjective MEs during the presentation of a standardised 'cold' stimulus in comparison with the effect observed during externally generated movement. A repeated-measures ANOVA showed a significant main effect for the 'movement' factor ($F_{1,13} = 7.59$, $p < 0.05$)

Table 1. Mean magnitude estimations (with standard deviations in parentheses) during self-generated and externally generated movements (larger means indicate more 'coldness' perceived).

	Self-generated movement	Externally generated movement
Trial 1: mean	4.21 (2.03)	4.99 (2.85)
Trial 2: mean	3.87 (2.50)	4.74 (2.48)
Trial 3: mean	3.55 (2.87)	4.91 (3.02)
Total: mean	3.88 (2.44)	4.88 (2.72)

with participants rating a self-produced 'cold' sensation on their right index finger as being significantly less intense than the same stimulus moved by an experimenter. MEs were not modulated by the 'trials' factor ($F_{2,26} = 0.53$, $p > 0.10$). In the current study, neither the trials main effect nor its interaction with the movement factor ($F_{2,26} = 0.19$, $p > 0.10$) reached statistical significance. The trials factor was of less interest than the movement factor but was included to test for possible time-related effects, and as a means of partitioning variance otherwise attributable to error.

4 Discussion

Consistent with the findings of earlier experiments (eg Blakemore et al 1998c), when movement was self-controlled the stimulus was reported as feeling less intense than when movement was externally generated. The results support the hypothesis that self-generated movement attenuates the perception of a 'cold' stimulus. This may also support the hypothesis that there is a corollary discharge mechanism in thermotactile perception.

The perception of 'cold' does not seem to be determined solely by stimulus – response relations. The ability to produce this outcome stands in contrast with McKemy et al's (2002) account in which innocuous cool results simply from raising the intracellular Ca^{2+} level of thinly myelinated Aδ fibres. The current data are consistent with the account of Jordan (1999) who suggested that participants "use copies of top – down motor commands (ie efference copies) to discriminate bottom – up afference into exafference (ie world movement) and reafference (ie self-movement)" (page 69).

Inspection of the experimental data indicates that, although the stimulation at the receptor sites of the right index finger was held constant between conditions and participants, the conscious experience of cold was significantly different for self-generated and externally generated movements. As self-generated and externally generated movement had quantitatively dissimilar effects on MEs, afferent mechanisms are insufficient to account for the changes during movement (Blakemore et al 1998c).

Magee and Kennedy (1980) state that unguided (self-generated) movement requires an "act of planning" that overburdens "the limited resources of the haptic system" (page 288). In their experiment, guided (externally generated) movement led to improved identification of raised-line drawings. Our results are consistent with an alternative explanation in which unguided (active) participants may have experienced an attenuated form of the stimulus, and thus were less capable of determining its features. It could also be stated that attention and attenuation are not mutually exclusive explanations of Magee and Kennedy's (1980) data. Mialet and Pichot (1980) suggest that attentional dysfunction may be the result of an inability to create "an internal representation of continued motion by means of the corollary discharge" (page 325). Corollary discharge may be a plausible explanation for the superiority of some guided over unguided haptic exploration, but additional work is needed to determine whether this is so.

In summary, when participants moved a 'cold' stimulus across their finger the stimulus was reported as feeling less intense than when movement was externally generated.

The findings suggest that efferent mechanisms (corollary discharge) may be an important aspect in 'cold' perception.

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