LETTER

REPLY TO MATHÔT AND NABER:
Neuroimaging shows that pupil mimicry is a social phenomenon

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We recently reported that an individual's pupils mimic changes in the pupils of his or her interaction partner, that mimicking dilating pupils associates with more trust in economic games, and that such pupil mimicry-related trust tracked neural activation in brain areas associated with theory of mind (1). Our findings confirm earlier studies suggesting that pupil mimicry is a social phenomenon (2–8). Mathôt and Naber (9) question this interpretation, suspecting that differences in luminance in dilating pupils compared with constricting pupils account for the observed effects. They provide some backup for their claim with citation of a study by Derksen et al. (10), in which they examined luminance-controlled stimuli.

We find the critique unconvincing. First, the stimuli used in the study by Derksen et al. (10) are arguably nonnatural (i.e., gray pupils) and thus different from the black pupil stimuli used in our studies. Second, effects of pupil mimicry on social behavior, such as trust, are consistently moderated by social context, including own-versus-partner ethnicity (2, 5, 10), own-versus-other species (7), or a cooperative-versus-competitive context (8). Such influence by social context is difficult to explain in terms of luminance effects only. Third, in the alternative proposed by Mathôt and Naber (9), partners' dilating pupils should result in higher social network activation (social attention), irrespective of whether participants mimic; in contrast, we find that pupil mimicry is required for social brain networks to activate. Thus, pupil mimicry contributes to social network activation that governs social attention, rather than vice versa. Lastly, Mathôt and Naber (9) suggest that attentional mechanisms are at play when processing the pupillary cues of others. Although our neuroimaging results (1) are not inconsistent with this possibility, when analyzing the eye movements, we found no difference in looking times when participants observe a partner's dilating pupils compared with constricting pupils [refer to refs. 1 (see Table 1) and 8]. Looking times were also similar during trials in which participants mimicked the observed pupil sizes compared with when they did not. Since participants were fixating at the eyes about 90% of the time and independent of the pupil size of their partner or their own reaction to that, we rule out that differences in attention modulated the extent to which participants' pupils reacted to changes in luminance on the computer screen (Table 2). At the brain level, visual areas (V5) [i.e., areas related to luminance (11)] activate when participants observe both pupil dilation and pupil constriction in another person. Crucially, when participants mimicked the observed pupil size compared with when they did not, we find increased activation in social brain regions associated with theory of mind (1).

In sum, we have direct and indirect evidence that pupil mimicry is both influenced by social context and related to activation in social brain networks. We not only concur with Mathôt and Naber that "there must be a social component somewhere in the chain of events that leads up to pupil mimicry" (9) but believe that, in our study (1), we have uncovered this social component at the levels of the brain and the ensuing social decision making.

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Table 1. Looking times on the eye region

Factors	*F*	df1	df2	Estimate	SE	Z	*P* value
Corrected model	1.601	3	3,376				0.187
Fixed factors							
Pupil partner	2.112	1	3,376				0.146
Mimicry	0.072	1	3,376				0.788
Pupil partner * mimicry	2.578	1	3,376				0.108
Random							
Intercept (subject = ID * session) variance	0.489	0.002	195.707	0.489	0.002	195.707	0.000

Multilevel model with the fixed factors of partner pupil (stimulus type: partner's pupils dilated, remained static, or constricted), mimicry (participant's response: mimicry or no mimicry), and pupil partner * mimicry; and with the random factor of intercept for subject. Looking times reflect the total dwell time in milliseconds spent on the eye region.

Table 2. Percentage looking times on the eye region

Factors	*F*	df1	df2	Estimate	SE	Z	*P* value
Corrected model	0.554	3	3,370				0.645
Fixed factors							
Pupil partner	0.932	1	3,370				0.334
Mimicry	0.008	1	3,370				0.929
Pupil partner * mimicry	0.706	1	3,370				0.401
Random factor							
Intercept (subject = ID * session) variance	0.044	0.002	40.382	0.044	0.002	40.382	0.000

Multilevel model with the fixed factors of partner pupil (stimuli type: partner's pupils dilated, remained static, or constricted), mimicry (participant's response: mimicry or no mimicry), and pupil partner * mimicry; and with the random factor of intercept for subject. The percentage of looking times on the eye region was computed by dividing the fixation dwell time that fell on the eye region compared with the total dwell time.

1 Prochazkova E, et al. (2018) Pupil mimicry promotes trust through the theory-of-mind network. *Proc Natl Acad Sci USA* 115:E7265–E7274.
2 Kret ME, Fischer AH, De Dreu CKW (2015) Pupil mimicry correlates with trust in in-group partners with dilating pupils. *Psychol Sci* 26:1401–1410.
3 Fawcett C, Wesevich V, Gredebäck G (2016) Pupillary contagion in infancy: Evidence for spontaneous transfer of arousal. *Psychol Sci* 27:997–1003.
4 Hess EH (1975) The role of pupil size in communication. *Sci Am* 233:110–112, 116–119.
5 Kret ME, De Dreu CKW (2017) Pupil-mimicry conditions trust in partners: Moderation by oxytocin and group membership. *Proc Biol Sci* 284:20162554.
6 Harrison NA, Singer T, Rotshtein P, Dolan RJ, Critchley HD (2006) Pupillary contagion: Central mechanisms engaged in sadness processing. *Soc Cogn Affect Neurosci* 1:5–17.
7 Kret ME, Tomonaga M, Matsuzawa T (2014) Chimpanzees and humans mimic pupil-size of conspecifics. *PLoS One* 9:e104886.
8 van Breen JA, De Dreu CKW, Kret ME (2018) Pupil to pupil: The effect of a partner's pupil size on (dis)honest behavior. *J Exp Soc Psychol* 74:231–245.
9 Mathôt S, Naber M (2018) There is no evidence that pupil mimicry is a social phenomenon. *Proc Natl Acad Sci USA* 115:E11565.
10 Derksen M, van Alphen J, Schaap S, Mathot S, Naber M (2018) Pupil mimicry is the result of brightness perception of the iris and pupil. *J Cogn* 1:32.
11 Seiffert AE, Somers DC, Dale AM, Tootell RB (2003) Functional MRI studies of human visual motion perception: Texture, luminance, attention and after-effects. *Cereb Cortex* 13:340–349.